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ROTHSCHILD, G. H. L.

The Biology of *Conomelus anceps* Germar (Homoptera: Delphacidae)

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TRANSACTIONS OF THE SOCIETY FOR BRITISH ENTOMOLOGY

VOL. 16 · DECEMBER 1964 PART V

The Biology of *Conomelus anceps* Germar (Homoptera : Delphacidae)

By G. H. L. Rothschild

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I. Introduction and Acknowledgments

From 1959 to 1961 a quantitative study was made of a population of *Conomelus anceps* Germar, a Delphacid occurring in *Juncus* areas at the Imperial College Field Station, Silwood Park, Ascot, Berks. The life history and reproductive biology of the Delphacid were studied in the course of this work, and are described here. The general life cycle of *Conomelus* has been described by Hassan (1939), and more recently by Whalley (1958) who has also studied the factors involved in the diapause of the egg stage.

C. anceps occurs only on members of the Juncaceae, and is widespread and common in the British Isles, the remainder of Europe, and North Africa (Le Quesne, 1960). The species has previously been known both as *Conomelus limbata* Fab. and *Liburnia limbata* Fab.

I am indebted to the following members of staff of the Imperial College Department of Zoology and Applied Entomology,

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for assistance in this work; Professor O. W. Richards for granting facilities at Silwood Park, and for his supervision and encouragement; Drs. J. P. Dempster, T. R. E. Southwood, N. Waloff, Mr. M. J. Way, and Mr. W. O. Steel, for their kind advice and for the loan of literature. I also wish to thank Mr. P. E. S. Whalley of the British Museum (Natural History) for generously making available his unpublished data on *Conomelus*. This work was financed by a grant from the Agricultural Research Council whose generosity is gratefully acknowledged.

II. Methods

Conomelus nymphs and adults were reared on *Juncus* plants grown in 3 and 6-inch diameter plant pots; the cages over these pots were either glass bell-jars or cellulose acetate cylinders, fitted with muslin covers. Others were reared on pieces of rush stem in 3 x 1 inch tubes; the tubes contained a basal layer of plaster of paris to reduce condensation. Nymphs were also reared from eggs kept on moist filter paper in Petri-dishes.

The reproductive organs were studied by dissecting fresh material in Ringer's solution and preserved material in Bouin's fluid. Individual Delphacids were weighed on a torsion balance (weighing to 0·01 mg.) within one hour of capture to prevent undue weight loss.

III. Description of Stages

Egg: has been described by Hassan (1939).

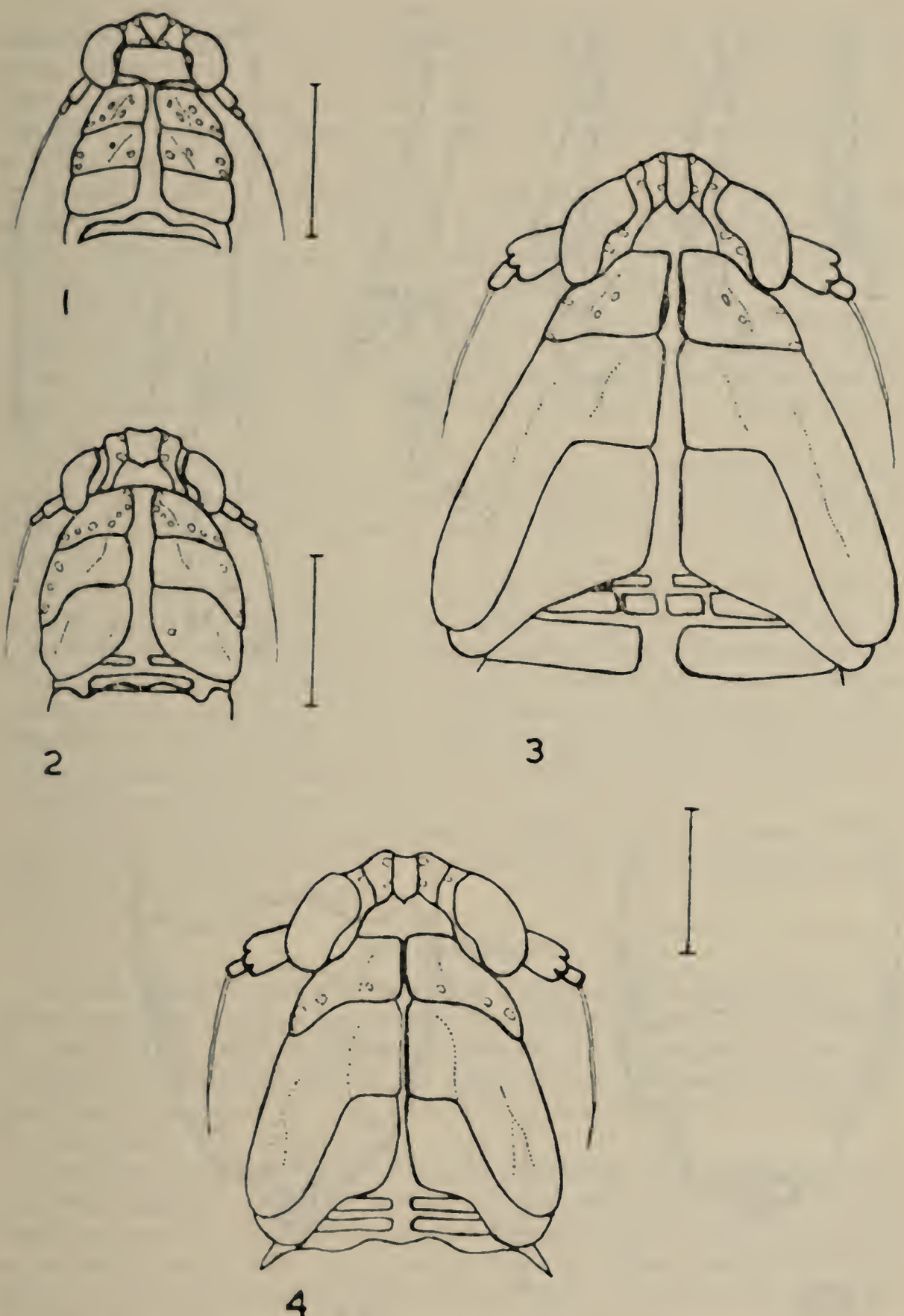
Nymphal stages: the only previously published description is that of the fourth instar (Hassan, 1939); Whalley (1958) has used measurements of tibial-length to separate the nymphs of both *Conomelus* and a *Delphacodes* species. In the present study the five nymphal instars have been separated by using measurements of head-width and femur-length (Table I); body-length is, however, rather variable. The characters of the hind tibia and tarsus used by Williams (1957) to separate the nymphs of *Perkinsiella saccharicida* Kirk. are also present in *C. anceps* (Figs. 5-9).

TABLE I

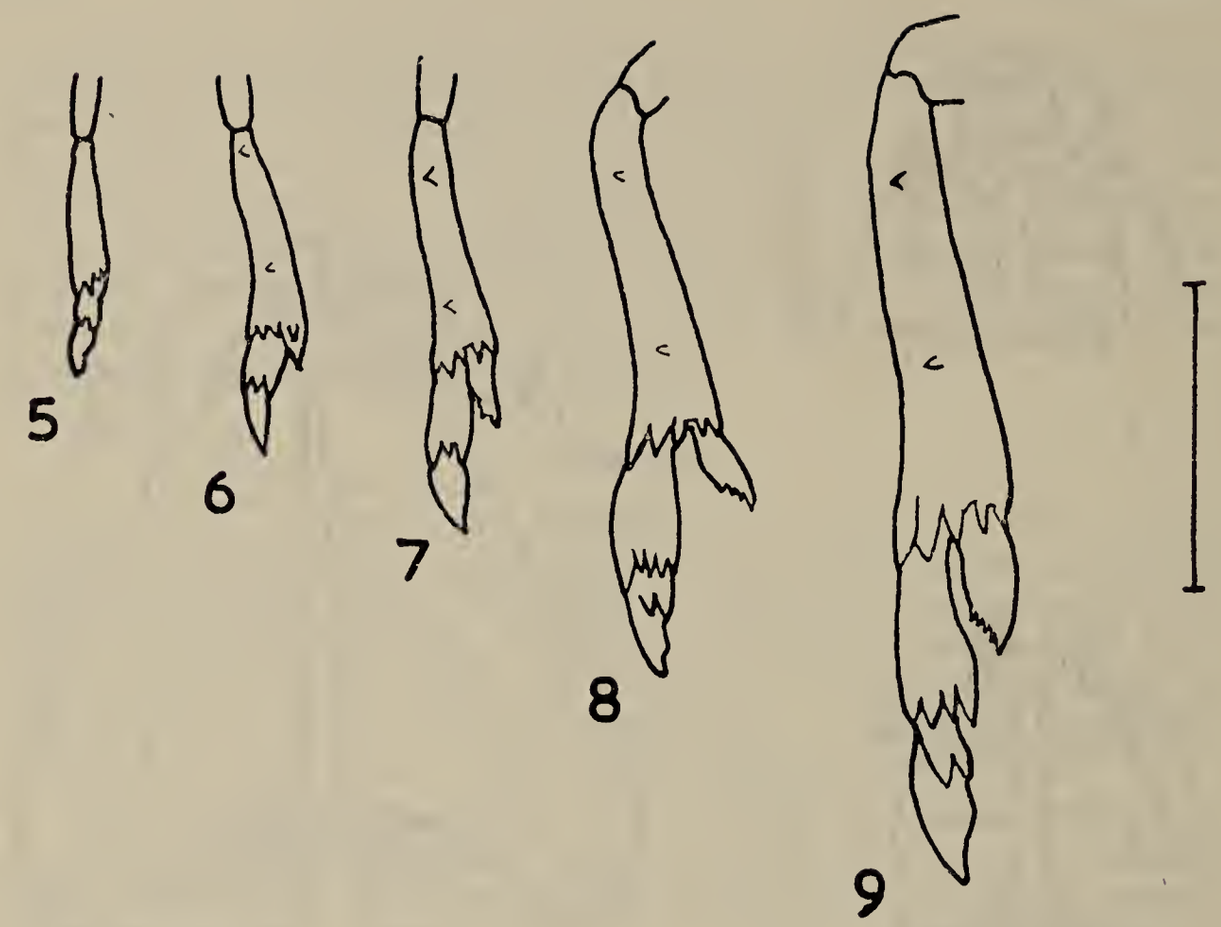
Measurements of head-width, femur-length, and body-length of the nymphs of *Conomelus anceps*

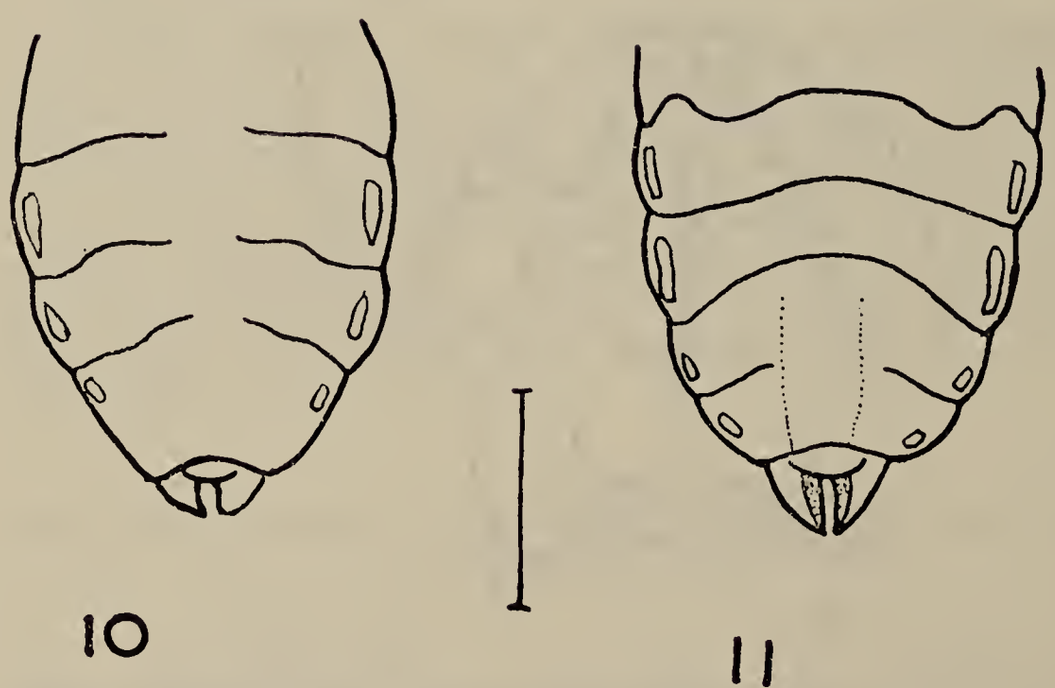
	Body-length			Head-width			Femur-Length		
Instar	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
First	1·05	0·77	1·20	0·31	0·27	0·35	0·15	0·15	0·17
Second	1·30	1·17	1·47	0·42	0·40	0·45	0·22	0·22	0·25
Third	1·53	1·27	1·70	0·52	0·50	0·55	0·31	0·30	0·32
Fourth	2·05	1·70	2·25	0·66	0·62	0·70	0·42	0·40	0·45
Fifth	2·62	2·45	2·90	0·85	0·80	0·90	0·60	0·60	0·65

Measurements in mm. (10 individuals of each instar)



Figs. 1-4.—*Conomelus anceps*: head and thorax of (1) first-instar nymph (scale = 0·2 mm.); (2) third-instar nymph; (3) fifth-instar nymph (macropter); (4) fifth-instar nymph (brachypter). (Scale in each case = 0·5 mm.)





Figs. 5-9.—*Conomelus anceps*: hind tibia and tarsus of (5) first-instar nymph; (6) second-instar nymph; (7) third-instar nymph; (8) fourth-instar nymph; (9) fifth-instar nymph. (Scale in each case=0·5 mm.). Figs. 10-11.—*Conomelus anceps*: ventral view of posterior abdominal segments of (10) fifth-instar nymph (male); (11) fifth-instar nymph (female). (Scale in each case = 0·5 mm.)

First instar (fig. 1): mean length 1·05 mm. Grey intersegmental areas and foveae of head and thorax, pale; median facial keels darker grey; eyes reddish. Legs pale grey with terminal part of femur and tarsal joints dark; hind tibia with four spines distally; tarsus two-segmented, with the first tarsal segment bearing four spines distally (fig. 5).

Second instar: mean length 1·30 mm. Coloration as first instar, but borders of thoracic and abdominal sclerites darker grey. Hind tibia with a distal articulated spur and two spines, one basal and another in the distal one-third (fig. 6).

Third instar (fig. 2): mean length, 1·53 mm. Greyish-brown, with pale areas on abdominal tergites. Eyes reddish-brown. Hind tibia with five distal spines; distal articulated spur bears two to three minute spines; first tarsal segment with five distal spines (fig. 7).

Fourth instar: mean length 2·05 mm. Coloration as third instar. Articulated spur of hind tibia bears four to five minute spines; second tarsal segment with two or three small spines (fig.8).

Fifth instar (figs. 3-4): mean length 2·62 mm. Pale greyish-brown with pale markings on most tergites. Wing-pads of macropterous nymphs (fig. 3) longer than those of brachypterous forms (fig. 4). Articulated tibial spur bears numerous minute spines; hind tarsus with three segments; the first segment bears five to six distal spines, the second three to four spines (fig. 9). The nymphs can be sexed by the structure of the terminal abdominal segments (figs. 10-11).

Adult: is described by Edwards (1896) and Le Quesne (1960). Most of the adults taken at Silwood Park were brachypterous, and only 7-10% were winged.

IV. Foodplants

In the present study *Conomelus* nymphs and adults have only been found on *Juncus effusus* in the field, although *J. articulatus* is accepted in the laboratory. Hassan (1939) reared *Conomelus* through to the adult stage on grass stems (species not stated), but found that adults only survived a few days when restricted to this food.

Fourth and fifth instar nymphs generally feed on all parts of the rush stems, while the earlier instars are mainly found in the basal six inches. Nymphs and adults may feed at any one point on a stem for periods up to three hours, unless disturbed when they run rapidly downwards or move out of sight to the opposite side of the stem.

V. Life History

The life cycle may be outlined as follows: eggs are laid in *Juncus* stems in late summer, from the end of July until the first week in September; overwintering occurs in the egg stage. The nymphs hatch in the following May, and after passing through five nymphal instars turn to the first adults in late June. There is generally only one generation per annum, but occasionally a

partial second generation may arise from the few eggs that do not overwinter.

Oviposition

The mean number of eggs laid by brachypterous females in the laboratory at 16±2°C is 29·9 with a maximum of 56 and a minimum of 10 eggs per female (25 females); the mean number of eggs laid per day is 2·43 with a maximum of 22 eggs per day; macropterous females lay an average of 23·0 eggs with a maximum of 29 and a minimum of 18 eggs per female (three females). An estimate of fecundity in the field has been obtained by calculating the number of eggs laid per unit area, and dividing this figure by the number of females produced per unit area throughout the season (calculated by the regression technique of Richards and Waloff, 1954); in 1960 an estimate of 42·0 eggs per female was obtained, and in 1961 39·6 per female. In view of the sampling errors involved in obtaining the field estimates, it is almost certain that the egg-laying potential is greater than has been calculated. The number of eggs laid per female is positively correlated with the duration of the egg-laying period ($r = 0{\cdot}6146$ $P < 0{\cdot}001$); the mean duration of the egg-laying period is 23 days with a maximum of 24 days and a minimum of 1 day (25 females); an estimate of the duration of the egg-laying period in the field has been obtained from the length of the peak oviposition period, i.e. 24 days in 1961 (15th August-8th September); the length of the egg-laying period, itself, is positively correlated with the longevity ($r = 0{\cdot}8031$ $P < 0{\cdot}001$). There is no correlation between the number of eggs laid and the duration of the preoviposition period ($r = 0{\cdot}0484$).

At Silwood Park, eggs have only been found in stems of *J. effusus*; eggs have not been found in *J. articulatus,* the only other *Juncus* species in the area studied. Whalley (1958) has, however, recorded egg sites in *J. inflexus, J maritima* and *J. conglomeratus.*

The egg sites of *Conomelus* have been described by Bakkendorf (1934) and Hassan (1939). Eggs are generally laid in the basal six inches of the stem, above the leaf-sheath; occasionally eggs are laid in the leaf-sheath, or high up on the stem up to 24 inches above the leaf-sheath. Egg mortality in the upper part of the stem is high, as this region tends to dry out or rot, and breaks up by the following spring. The mean number of eggs laid per site is 2·86 with a maximum of 7 and a minimum of 1 per site.

TABLE II.

Relationship between stem diameter and number of eggs per stem

Stem diameter in mm.	% of total stems	Mean No. of sites/stem	% of total sites
0·84-1·05	12·36	108	15·32
1·05-1·26	31·46	125	17·73
1·26-1·47	29·31	132	18·72
1·47-1·68	21·47	214	30·35
1·68-1·89	4·49	127	18·01

Ovipositing females appear to choose the larger stems (Table II); more eggs are laid in stems having a diameter of 1·47-1·89 mm. than would be expected from random oviposition.

Nymphal Development

Nymphs begin to emerge in early May, and continue to do so for about four to five weeks. Whalley (1958) has shown that most eggs enter a complete diapause; he obtained a 100% hatch from eggs that were kept at 3-10°C for several days and were then restored to 25°C.; of several hundred eggs kept at a constant temperature of 25°C., without a cool spell, only two hatched. It is, therefore, possible for some nymphs to hatch in the field before the winter months, and give rise to a partial second generation: this may account for the few third-instar nymphs that were found in the field in September 1960 at Silwood Park, and also for a few adults found in January 1960.

The nymph emerges by forcing off the operculum of the egg, and is translucent when newly-emerged; the final coloration is attained after about 30 minutes. In the insectary a 5% hatching failure was recorded; in most of these cases the nymphs had emerged from the chorion, but were unable to break through the embryonic membranes. Examination of egg sites in the field showed that most nymphs emerged successfully. First-instar nymphs generally aggregate in the basal six inches of the stems, but it is not clear whether this is due to actual gregariousness or merely due to the high density of egg sites in this part of the stem. Nymphs emerging from eggs laid high up on the rush stems always move down into the basal regions as soon as they have attained their final coloration. Nymphs nearing a moult are easily recognised as the thoracic sclerites are widely separated in the mid-line. When about to moult nymphs face upwards and grip the stem with the tarsal claws only; the rostrum is not inserted.

Hassan (1939) has noted the duration of the various nymphal instars of *Conomelus* (rearing temperature not recorded), and his data are compared with those obtained in the present study (Table III).

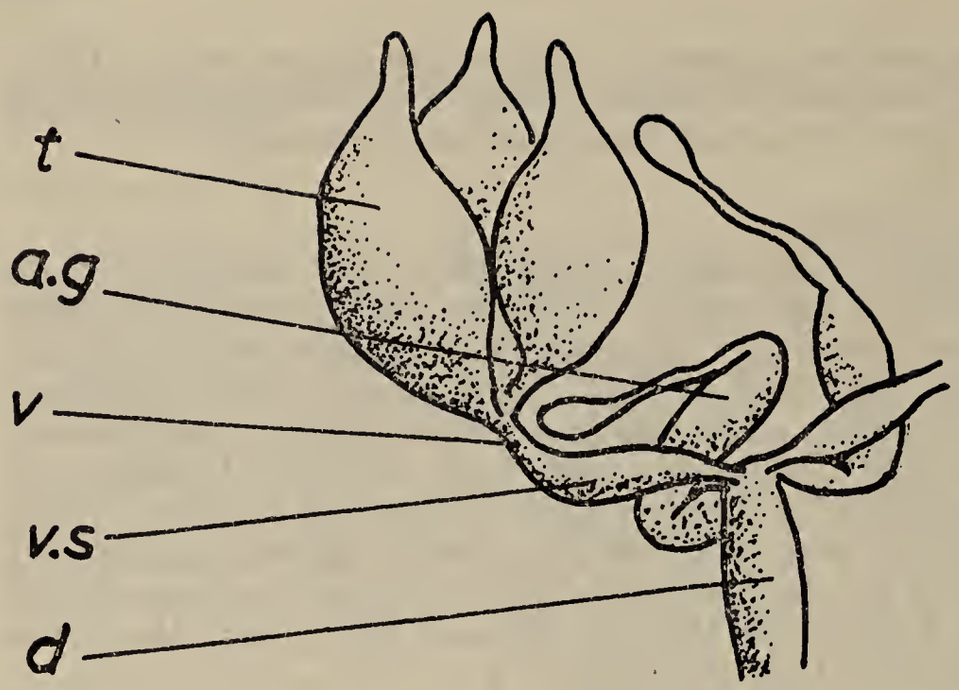
TABLE III

Length of instars in days at 16±2°C.

Instar	Minimum	Mean	Maximum
First	5 (8)	10·1 (11)	19 (14)
Second	4 (6)	9·0 (9)	15 (11)
Third	6 (4)	8·0 (7)	12 (10)
Fourth	6 (2)	10·9 (3)	15 (4)
Fifth	10 (4)	10·8 (7)	16 (9)
Total	31 (24)	48·8 (37)	77 (48)

Hassan's (1939) data in brackets

The estimated total duration of the nymphal stages in the field was 53 days in 1960 and 59 days in 1961. The difference between



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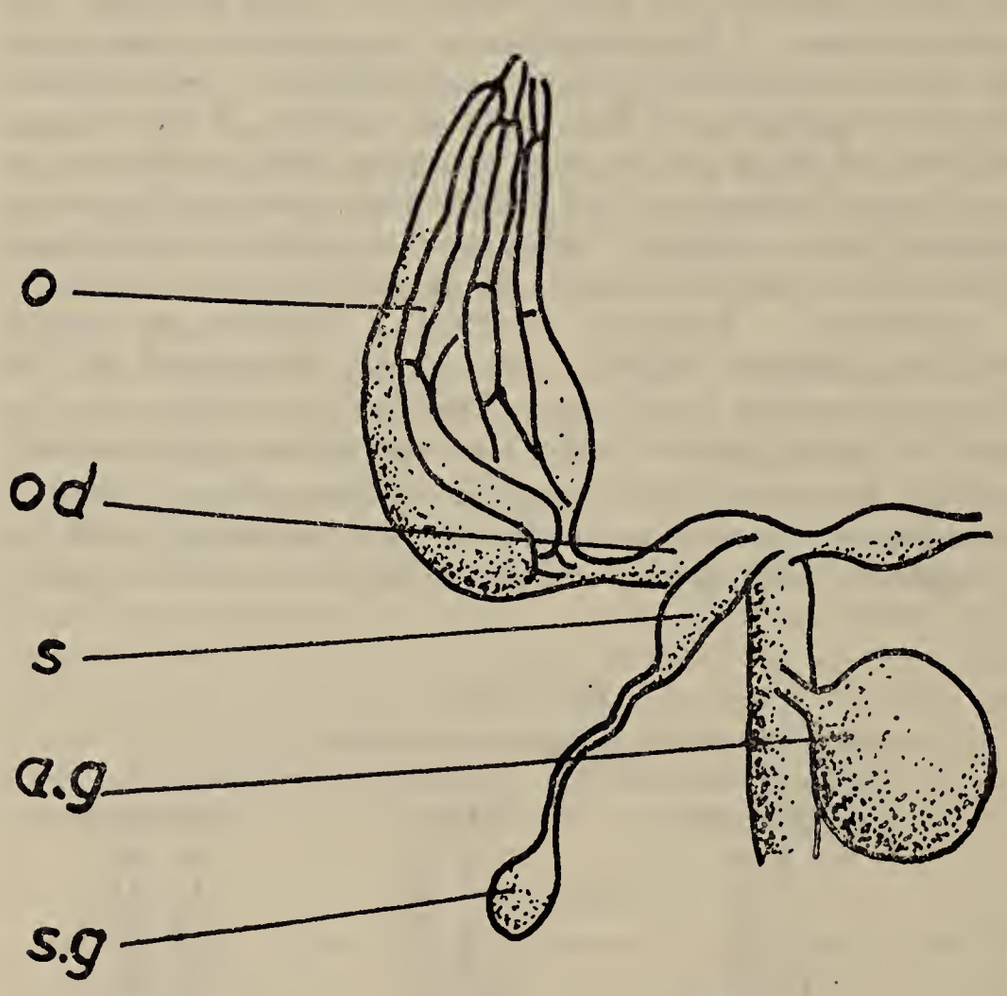

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Figs. 12-13.—*Conomelus anceps*: reproductive organs of (12) adult male; t., testis; a.g., accessory gland; d., ductus ejaculatorius; v., vas deferens; v.s., vesicula seminalis; (13) adult female; a.g., accessory gland; o., ovary; od., oviduct; s.g., spermathecal gland; s., spermatheca. (Scale in each case = 1·0 mm.)

the field and insectary figures was probably due to the lower field temperatures, i.e. 12·7 °C in 1960 and 14·1 °C in 1961; the difference in the total length of the nymphal instars in the field in 1960 and 1961 cannot be related to temperature.

Adult Development

The newly-moulted adult is white and attains the final coloration after about one to two hours.

Sexual maturation: The female reproductive organs (fig. 13) consist of a pair of ovaries each with an average of 11 ovarioles (maximum 14 and minimum 10, based on 72 females). In a few instances ovariole asymmetry was recorded, with 11 ovarioles in one ovary and 12 in the other (also 10 + 11 ovarioles). Each ovariole may contain up to four follicles. The mature ovaries fill most of the body cavity.

The male organs (fig. 12) consist of paired testes, each comprising three pear-shaped follicles. The paired vasa deferentia widen terminally to form the vesiculae seminales, which in turn join the ductus ejaculatorius. Also joining the latter are a pair of convoluted accessory glands. The testis sheath and hypodermal layer of the abdomen contain a yellowish pigment; *Conomelus* females contain little or no pigment. By this feature nymphs can generally be sexed from the third-instar onwards.

Table IV shows the growth rate of the male reproductive organs (in brachypters) throughout the season in the field.

TABLE IV

Seasonal development of reproductive organs of brachypterous males in the field

Date	Testes			Accessory gland		Ductus ejaculatorius		Vas deferens		Mean weight in mg. (of 20 males)
	Length	Width	Thick-ness	Length	Width	Length	Width	Length	Width	
5/7	1·40	0·49	0·13	1·70	0·11	0·57	0·14	1·03	0·07	1·51
17/7	1·45	0·52	0·22	1·78	0·11	0·69	0·15	1·01	0·07	1·57
29/7	1·48	0·50	0·19	1·89	0·14	0·68	0·17	1·01	0·11	1·66
16/8	1·74	0·51	0·25	2·28	0·18	0·78	0·20	1·45	0·10	1·87
30/8	1·61	0·71	0·25	2·85	0·27	0·99	0·18	1·61	0·15	1·88
13/9	1·46	0·68	0·23	2·74	0·21	0·97	0·20	1·75	0·13	1·94
13/10	1·20	0·55	0·11	3·25	0·27	1·03	0·24	1·77	0·12	1·81
1/11	0·85	0·37	0·06	3·24	0·30	0·97	0·28	1·69	0·11	—

Measurements in mm. taken in 1961 (mean of individuals)

Sperms are already present in the testes of fifth-instar nymphs, but these are not yet motile. Although *Conomelus* males mature fairly rapidly and may copulate within 14 days of emergence, the reproductive organs continue to grow until the second or third week in August. At this stage the testes reach their maximum size; the accessory glands, however, increase noticeably in size throughout the entire season, while the ductus ejaculatorius

and vasa deferentia also show slight increases in length over this period. From September onwards the testes decrease in size; the testes of males dissected in November had degenerated to such an extent that they were only distinguished with difficulty from the fat body.

In the female, maturation is less rapid; the mean length of the preoviposition period at 16±2°C is 25 days, with a maximum of 36 days and a minimum of 18 days (40 females). In the field the estimated length of the preoviposition period in 1961 was 29 days; this figure was calculated from the date of appearance of the first adults, and the first eggs, in the field (22nd June-21st July). Sperms have been found in the spermathecae of females with poorly-developed ovaries, but males will not pair with newly-emerged females. Table V shows the seasonal development of the female reproductive organs (in brachypters).

TABLE V

Seasonal development of reproductive organs of brachypterous females in the field.

Date	Ovarioles		No. eggs in ovaries per female	Oviduct		Accessory gland	Spermatheca		
	Length	Width		Length	Width	Diameter	Length	Width	Mean weight in mg. (20 individuals)
5/7	0·92	0·05	0	0·61	0·11	0·58	0·58	0·13	1·74
17/7	0·83	0·05	1·37	0·62	0·07	0·51	0·53	0·11	1·73
29/7	1·14	0·05	2·00	0·60	0·09	0·50	0·46	0·11	2·00
5/8	1·73	0·06	5·60	0·76	0·10	0·64	0·62	0·13	2·09
16/8	1·91	0·20	9·00	0·59	0·14	0·65	0·57	0·13	2·48
30/8	1·76	0·11	11·80	0·75	0·11	0·79	0·62	0·14	2·79
13/9	2·08	plus eggs	12·40	0·74	0·12	0·91	0·63	0·14	2·90
3/10	2·06	„ „	13·60	0·76	0·12	0·98	0·58	0·14	3·07

Measurements in mm. taken in 1961 (mean of 10 individuals)

The ovarioles of newly-emerged females are small and thread-like, measuring as little as 0·03 mm. in width; they gradually increase in size as maturation occurs and ripe eggs are produced. In immature females, much of the abdomen is filled with a rather diffuse, fat body which decreases in size as the ovaries develop. Ripe eggs first appear in the lateral oviducts in mid-July, and the mean number of eggs increases throughout the season reaching 12·0 during the peak oviposition period. The maximum number of eggs found in a female was 23, 12 eggs in one ovary and 11 in the other. Maturation of successive eggs in a single ovariole is slow, and the second oocyte is still poorly developed when the first egg ripens. Egg-laying, is, however, almost continuous as all the ovarioles do not produce eggs simultaneously.

Other parts of the female reproductive system also increase in size throughout the season, particularly the accessory gland, which becomes distended with a viscous material; the spermatheca and

oviducts also show slight increases in size during this period (Table V). At the end of the season, in October, the ovaries show no signs of degeneration and contain at least 13 ripe eggs; as very few fifth-instar nymphs are taken later than the end of August, these females must be at least 60 days old. Degeneration of the ovaries has been recorded in various insect orders. Phipps (1949) gives an account of these changes in grasshoppers, and suggests that the degeneration is due to lack of food at the end of the season. Richards and Waloff (1954), however, consider that the age of the female affects the rate of yolk production, as old females with an ample food supply die with the ovarioles containing little yolk. The normal condition of the ovaries and the increase in the number of ovariole eggs, in the presence of an ample food supply, indicate that the normal degeneration pattern does not occur in *Conomelus*. Females collected in the field throughout October never laid eggs in the insectary, and died after varying periods of time with their bodies greatly distended with eggs. It appears that while, for some unknown reason, the oviposition urge is lost, the female continues to produce more eggs resulting in the utilisation of any remaining reserve materials, and ending in exhaustion and death. Johanssen (1958) has

TABLE VI

Seasonal development of reproductive organs of macropterous males in the Field

Date	Testes		Accessory gland	Vas deferens	Ductus ejaculatorius	Weight in mgs.
	Length	Width	Length	Length	Length	
17/7	1·09 (3)	0·46	1·34	1·15	0·60	1·29 (1)
29/7	1·15 (5)	0·49	1·15	1·01	0·65	1·37 (1)
16/8	0·99 (3)	0·58	1·59	1·05	0·59	1·41 (4)
30/8	1·03 (5)	0·53	1·75	0·97	0·65	1·32 (4)
13/9	1·17 (2)	0·46	2·41	1·40	0·64	—

Measurements in mm. taken in 1961 (number of individuals in brackets)

TABLE VII

Seasonal development of reproductive organs of macropterous females in the Field

Date	No. eggs per female	Ovariole	Spermatheca	Oviduct	Accessory gland	Weight in mgs.
		Type	Diameter	Length	Length	
17/7	— (4)	undeveloped	0·48	0·41	0·46	1·58 (2)
29/7	— (9)	,,	0·41	0·56	0·52	1·57 (4)
16/8	— (10)	,,	0·42	0·53	0·53	1·62 (9)
30/8	— (10)	,,	0·45	0·62	0·57	1·88 (4)
13/9	10·3 (6)	With ripe eggs	0·65	0·79	0·53	—

Measurements in mm. taken in 1961 (number of individuals in brackets)

observed this phenomenon in the milkweed bug *Oncopeltus fasciatus* (Dallas), although only in two instances. In each case the adult died with the abdomen so fully distended with eggs that the hind-gut was constricted, and Johanssen concluded that starvation was the cause of death; he does not, suggest any reason for the initial oviposition failure.

The development of the reproductive organs of macropterous adults is shown in Tables VI and VII. The mature reproductive organs of both male and female macropters are smaller, and slower to develop, than those of the brachypters; this may be due to the flight muscles developing at the expense of the reproductive organs.

Tables IV-VII relate weight changes to sexual maturation in the adults. The brachypterous males attain a mean weight of 1·87 mg. relatively early in the season, and then remain at, or fluctuate around, this weight. Most of this increase is due to the development of the testes and accessory glands. In spite of the testicular degeneration of senescent males there is only a slight decrease in weight at the end of the season; this is due to the continued growth of the accessory glands. The maximum weight attained by a male was 2·50 mg. The weight of female brachypters increases steadily throughout the season, due mainly to the growth of the accessory gland and the production of ripe eggs in the ovaries. Because of the retention of eggs by senescent females, the mean weight increases until the end of the season, when a peak of 3·07 mg. is reached. The maximum recorded weight of a *Conomelus* female was 3·92 mg. The weights of macropters are lower than those of brachypters, and can be directly related to the smaller reproductive organs (Tables VI-VII).

Sex-ratio and longevity: the mean sex-ratios of *Conomelus* adults produced throughout 1960 and 1961 are given in table VIII. The sex-ratio of the brachypters is fairly constant for the two years. The macropterous condition is generally more prevalent in females, but the ratios varied considerably in the two seasons. Males tended to emerge before the females, and the ratio of females to males in early July (1 female : 19 males in 1961) gradually increases throughout the season until the sex-ratio is reversed in late September (1·6 females : 1 male in 1961).

TABLE VIII

Mean sex-ratio of *Conomelus* adults in 1960 and 1961

Year	Wing form	Females	Ratio	Males
1960	Brachypter	1	:	1·5
1961	,,	1	:	1·62
1960	Macropter	1	:	1·31
1961	,,	1	:	0·36

The mean longevity of brachypterous females at 16±2°C is 38 days, with a maximum of 52 days and a minimum of 27 days;

the corresponding figures for macropters are 33, 36, and 29 days respectively. In the field a rough estimate of female longevity (brachypters) was obtained by noting the date of appearance of the first adult and the date when the adult population begins to decline, i.e. 36 days in 1960 and 43 days in 1961. The longevity of males at 16±2°C was 27 days, with a maximum of 42 and a minimum of 16 days. *Conomelus* adults are found in the field until October, and occasionally November, which indicates that longevity in the field may be at least 60 days.

VI. Summary

1. The life history and reproductive biology of the Delphacid, *Conomelus anceps* Germar are discussed. The immature stages are described, using measurements of head-width and femur-length to separate the instars.

2. Brachypterous females were found to lay an average of 30 eggs at 16±2°C. (maximum 56 eggs) in the laboratory, but in the field it was estimated that 40·8 eggs were laid per female; macropterous females lay an average of 23·0 eggs at 16±2°C. The number of eggs laid is positively correlated with the duration of the egg-laying period (mean duration 25·2 days at 16±2°C.).

3. At Silwood Park, eggs are only laid in *Juncus effusus* which is also the sole food-plant; eggs are generally laid in the basal six inches of the stems, above the leaf sheaths. The mean number of eggs per site is 2·9 with a maximum of 7 eggs per site. Eggs are laid from late July until early September, with a peak oviposition period in the last two weeks of August.

4. Nymphs emerge over a four to five-week period beginning in early May. The mean duration of individual instars at 16±2 C. is: first instar 10·1 days, second instar 9·0 days, third instar 8·0 days, fourth-instar 10·9 days, fifth-instar 10·8 days; total 48·8 days. The total duration of the nymphal stages in the field has been estimated as 53 days (1960) and 59 days (1961).

5. The reproductive organs and their developments are described. Males mature and may copulate within 14 days of emergence. Examination of samples of males from the field shows that the testes reach their maximum size in mid-August; the accessory glands, however, increase in size throughout the entire season. Females mature after a mean period of 25·2 days at 16±2° C., and after an estimated period of 29 days in the field. In addition to normal ovariole development, the accessory gland grows considerably throughout the entire season. Senescent females appear to lose the urge to oviposit, and die distended with eggs. The reproductive organs of macropters are smaller and slower to develop than those of brachypters.

6. The development of the reproductive organs is related to seasonal weight changes. Estimates of longevity in the field and laboratory are 39·5 and 38·3 respectively, for brachypterous females; the longevity of males in the laboratory averages 27 days. The mean longevity of macropterous females in the

laboratory is 32·7 days. Seasonal changes in the sex-ratio are described.

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